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Structural and functional organization of the '1S0.8 gene-rich region' in the Triticeae

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Abstract

Wheat genes are present in physically small, gene-rich regions, interspersed by gene-poor blocks of retrotransposon-like repetitive sequences. One of the largest gene-rich regions is present around fraction length (FL) 0.8 of the short arm of wheat homoeologous group 1 chromosomes and is called '1S0.8 region'. The objective of this study was to reveal the structural and functional organization of the '1S0.8 region' in various Triticeae and other Poaceae species. Consensus genetic linkage maps of the '1S0.8 region' were constructed for wheat, barley, and rye by combining mapping information from 16, 11, and 12 genetic linkage maps, respectively. The consensus genetic linkage maps were compared with each other and with a consensus physical map of wheat homoeologous group *1*. Comparative analyses localized 75 agronomically important genes to the '1S0.8 region'. This high-resolution comparison revealed exceptions to the rule of conserved gene synteny, established using low-resolution marker comparisons. Small rearrangements such as duplications, deletions, and inversions were observed among species. Proportion of chromosomal recombination occurring in the '1S0.8 region' was very similar among species. Within the gene-rich region, the extent of recombination was highly variable but the pattern was similar among species. Relative recombination among markers was similar except for a few loci where drastic differences were observed among species. Chromosomal rearrangements did not always change the extent of recombination for the region. Differences in gene order and relative recombination were the least between wheat and barley, and were the highest between wheat and oat.

Introduction

The Triticeae tribe belongs to the Poaceae family and contains more than 15 genera and 300 species including wheat, barley, and rye. Genomes of the cultivated Triticeae species are large. The genome of wheat, for example, is about 16 million kb, of which only 1–5% is expected to contain genes. Wheat genes are present in physically small gene-rich regions interspersed by large blocks of repetitive DNA (Gill *et al.*, 1996a, b; Sandhu, 2000; Sandhu *et al.*, 2001). The gene-poor regions are primarily composed of retrotransposon-like repetitive sequences (Barakat *et al.*, 1997; Feuillet and Keller, 1999). About three to four major and four to five minor gene-rich regions are present per chromosome. Physical location, structural organization, and gene densities of the gene-rich regions are similar among the three genomes of hexaploid wheat (Gill *et al.*, 1996a, b; Sandhu, 2000; Sandhu *et al.*, 2001). By deletion line-based physical mapping, it was possible to localize more than 90% of wheat genes to less than 10% of the chromosomal region (Gill *et al.*, 1996a; Sandhu, 2000). The precision of this localization depends upon the number of deletion lines and thus will increase with the availability of more deletion lines.

One of the largest, and perhaps most important, gene-rich region is present around fraction length (FL)

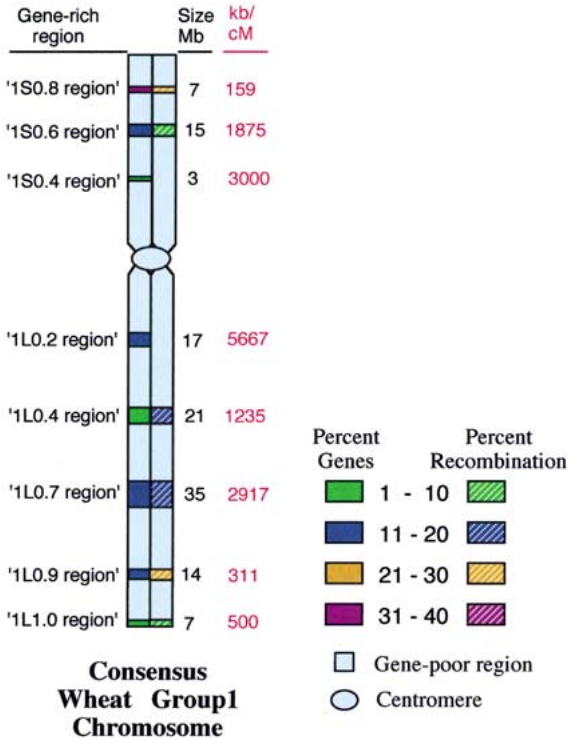

Figure 1. Distribution of genes and recombination on wheat homoeologous group 1 chromosomes. The consensus chromosome and the location and size of the gene-rich regions are drawn to scale, based on the average size of the three homoeologous chromosomes 1A, 1B, and 1D. Names of the gene-rich regions are given on the left side of the consensus chromosome. In the nomenclature of the gene-rich regions (e.g. 1S0.8), the first digit represents the wheat homoeologous group followed by the short arm (S) or long arm (L) letter. The last two numerals represent fraction length of the gene-rich region location. Actual physical size (black) and the ratio of physical to genetic distance (red) for a region are given on the right-hand side of the consensus chromosome. Sizes (in Mb) of gene-rich regions were calculated based on cytological measurements (measurements of the region bracketed by the flanking deletion line breakpoints in comparison to the total genome size in μ), and were drawn to scale. Percentage of genes in the gene-rich region was calculated from overlapping deletion line mapping results for 147 cDNA and *Pst*I genomic clones from 26 different libraries from 7 different species of the family Poaceae. Recombination in a chromosomal region was calculated by comparing the deletion line-based physical map with the consensus genetic linkage map of the Triticeae (Van Deynze *et al.*, 1995; Sandhu, 2000).

0.8 on the short arm of wheat homoeologous group 1 chromosomes ('1S0.8 region', Figure 1). The region is very small in size and is bracketed by deletion breakpoints. The region is best localized on chromosome 1B of wheat where it is bracketed by the breakpoints of deletion lines 1BS-4 and 1BS-18. On chromosome 1BS, the region lies in the middle of the satellite. The haploid wheat chromosome complement is about 235 μ in length (Gill *et al.*, 1991), containing 16 million kb of DNA (Bennett and Smith, 1976). The satellite region is about 1 μ long, translating to about 68 Mb of DNA. The '1S0.8 region' is about 7% of the satellite (between FL 0.47 and 0.54 of the satellite) (Gill *et al.*, 1991), which is equal to about 5 Mb. To compensate for additional markers mapping just outside the flanked part of the '1S0.8 region', the size estimate was assumed to be 7 Mb. A total of 46 markers have been identified for the '1S0.8 region' by comparative mapping followed by deletion line-based physical mapping (Sandhu *et al.*, 2001). Physically, the region is less than 1% of chromosome 1, but, based on a sample of 147 markers, seems to contain about 31% of the genes (Sandhu, 2000).

Comparisons of low-density genetic maps suggested that gene distribution and synteny are highly conserved among Triticeae species and moderately conserved among the members of family Poaceae. Physical mapping results suggested that the location and structural organization of this region are conserved among wheat genomes (Gill *et al.*, 1996a; Sandhu *et al.*, 2001). By aligning a few DNA and morphological markers across six cereal genomes, synteny among all grass genomes was predicted to be conserved at the chromosomal block level (Moore *et al.*, 1995). Comparisons of a few BAC clone sequences revealed small duplications, rearrangements, or other subtle differences that appear to be common among closely related genomes (Bennetzen *et al.*, 1998; Feuillet and Keller, 1999; J. Bennetzen, personal communication). All the above comparisons also established that the extent of gene synteny conservation is not uniform within a genome.

The objectives of this study were to investigate the structural and functional organization of the '1S0.8 region' in wheat and various other Triticeae and Poaceae species. Such an analysis will provide a measure for the extent and accuracy by which information and resources can be utilized across Triticeae species for structural and functional genomics.

Materials and methods

Comparative mapping

Sixteen genetic linkage maps for wheat (Lagudah *et al.*, 1991; Devey and Hart, 1993; Gill *et al.*, 1993; Dubcovsky and Dvorak, 1995; Dubcovsky *et al.*, 1995; Van Deynze *et al.*, 1995; Blanco *et al.*, 1998;

Boyko *et al.*, 1999; Spielmeyer *et al.*, 2000a, b), 11 for barley (Graner *et al.*, 1991, 1993; Kleinhofs *et al.*, 1993; Kjaer *et al.*, 1995; Langridge *et al.*, 1995; Bezant *et al.*, 1996; Qi *et al.*, 1996; Franckowiak, 1997; Jensen, 1999; Wei *et al.*, 1999; Miyazaki *et al.*, 2000), and 12 rye linkage maps (Lawrence and Appels, 1986; Benito *et al.*, 1990; Gaunt and Singh, 1990; Baum and Appels, 1991; Carrillo *et al.*, 1992; Wang *et al.*, 1992; Devos *et al.*, 1993; Devos, 1996, GrainGenes-http://wheat.pw.usda.gov; Wanous *et al.*, 1997; Borner and Korzun, 1998; Korzun *et al.*, 1998; Voylokov *et al.*, 1998), were used to construct consensus genetic linkage maps.

Markers used in maps were compared to determine predicted order of markers in Tables 1, 2, and 3. If the maps compared show contradiction then the marker order represented by the majority of the maps was considered. Any marker which is missing in a particular map is represented by a – sign. For a particular marker where the precise location was not shown on a genetic linkage map, flanking markers were used to determine range where that particular marker is located.

Construction of consensus genetic linkage maps

For the construction of consensus genetic linkage maps, maps were aligned and regions corresponding to the '1S0.8 region' on linkage maps were identified. The two most distant '1S0.8 region' markers were used for the demarcation of the genetic linkage maps for the region. To increase the accuracy of identifying '1S0.8 region' markers, a marker (*Xcdo1173*) for a proximal gene-rich region present at FL 0.6 was also included in the comparative analysis. Two genes (*Per1* and *Hk1*) were not flanked by '1S0.8 region' markers on the proximal side but were selected because of their tight linkage with *Xpsr381*. Similarly, four genes present on the proximal end of the barley consensus genetic linkage map were included based on their close linkage to a '1S0.8 region' marker, *Xabg500*. The marker loci common between two maps were used as anchors and the genetic distances for loci between anchor markers were extrapolated. Genetic distances used for the construction of genetic linkage maps are relative rather than absolute. For a discrepant order of markers, the order found in the majority of maps was selected for the construction of consensus genetic linkage maps.

Due to the lack of sufficient maps and common markers among the available maps, it was not possible to construct a reliable consensus genetic linkage map of oat. Therefore, Van Deynze's oat genetic linkage map was used for comparisons (Van Deynze *et al.*, 1995).

Results and discussion

Map comparisons

For comparisons of the '1S0.8 region' across the tribe, 40 Triticeae genetic linkage maps were compared. For each major crop species, a consensus map was developed using available maps. Marker order and recombination values for maps used in the construction of the consensus maps for wheat, barley and rye are shown in Tables 1, 2, and 3, respectively. The consensus maps for the '1S0.8 region' in wheat, barley, and rye consisted of 66, 61, and 24 marker loci, respectively. The genetic linkage map of oat consisted of 16 marker loci (Van Deynze *et al.*, 1995). The consensus genetic linkage maps and the oat map were compared with each other and with the physical map of chromosome 1BS of wheat. Thirty-nine of 46 '1S0.8 region' markers on the physical map were present on at least one of the linkage maps (Figure 2). Sixteen marker loci were common between wheat and barley consensus maps, 12 between wheat and rye, and six between wheat and oat.

Agronomically important genes in the '1S0.8 region' of Triticeae

Usefulness of the wheat homoeologous group 1 short arm was realized early on with the observations that the homoeologous arm from rye was spontaneously selected and thus is present in many of the high-yielding cultivars of the world. Later studies identified many useful genes on group *1S* homoeologous arm in rye and other Triticeae species. Comparisons of the consensus genetic linkage maps with the wheat physical maps revealed that a great majority of Triticeae chromosome 1S-specific agronomically important genes actually are located in the '1S0.8 gene-rich region' (Figure 2). Major gene classes present in the region include genes for disease resistance – leaf rust (*Lr21, Lr26*), stem rust (*Sr21, Sr31, Sr33*), yellow rust (*Yr4, Yr9, Yr15*), barley rust (*Pa4*), and powdery mildew (*Pm3, Pm8, Mla, Mlra, Mla6, Ml-Ru3, Mla13, Mla14, Mlk, Mlnn*) –, genes for grain quality – , gliadins *(Gli1, Gli3*), glutenin (*Glu3*), hordein (*Hor1, Hor2, Hor4, Hor5*), secalins (*Sec1*) and triticin (*Tri*) genes for male sterility (*msg4, msg31*), and restorers

Table 1. Genetic linkage maps of wheat for '1S0.8 region'. Markers are arranged in their predicted order. (-) represents missing marker in that particular map.

Predicted order of markers	'Van Deynze 95 1A'	'Van Deynze 1B'	'Van Deynze 1D'	'Dubcovsky 95 1A/1A^m'	'Boyko 99 1D'	'Blanco 98 1A'	'Dub 95 1A^m G1777 × G2528'	'Dub 95 1A^m G3116 × DV092'	'Spielmeyer 00 1D SSP'	'Speilmeyer 00 1D LR'	'Dubcovsky 95 1B'	'Gill 93 1D'	'Lagudah 91 1D'	'Hart 93 1A'	'Hart 93 1B'	'Hart 93 1D'
XksuD14a	0	0	-	-	0	-	-	-	-	-	-	-	-	-	-	-
Lr21	-	-	0	-	0-14	-	-	-	-	0	-	0	-	-	-	0
rgaYr10b	-	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-
Rg2	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	0
Bg	-	-	-	0	-	0	0	0	-	-	-	-	-	-	-	-
Hg	-	-	-	0	-	2	0	-	-	-	-	-	-	7	-	-
Pm3a	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-
rga5.2b	-	-	-	-	-	-	-	-	0	2	-	-	-	-	-	-
rgaYr10a	-	-	-	-	-	-	-	2	6	-	-	-	-	-	-	-
rga5.2a	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
Gli1a	5	0-15	0	2.6	0-14	3	1	1	3	8	0	7	0	0	0	5
Gli1b	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-
Gli1c	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-
Rg1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
XksuD14b	9	-	11	-	-	-	1	-	-	-	-	-	-	-	-	-
Xbcd1434	-	13	2.6	14	-	1	-	-	7	-	9	-	-	-	-	-
Xwhs179a	0-15	11-13	-	-	-	-	- 5	12	-	-	-	-	-	-	-	-
XksuD14c	-	-	13	-	-	-	-	-	-	-	-	21	-	-	-	-
Xmwg938	-	15	18	-	-	-	-	-	5	16	-	-	-	-	-	-
Glu3a	-	-	-	2,6	-	-	2	1	7	-	2	-	4	0	3	7
Xcdo426	19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xmwg920a	-	-	-	-	-	-	5	2	-	-	-	-	-	-	-	-
Xmwg920b	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Glu3b	-	-	-	-	-	-	-	-	9	-	-	-	-	-	-	-
Xwhs179b	-	-	18-27	-	-	-	-	-	9	18	-	-	-	-	-	-
Glu3c	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-
Xmwg837	-	0-15	27	-	-	-	-	-	-	-	-	-	-	-	-	-
Xmwg2021	-	-	-	2.6	-	-	7	3	-	21	14	-	-	-	-	-
Lrk10a	-	-	-	-	-	-	-	-	14	21	-	-	-	-	-	-
Lrk10b	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-
Xcmwg645	-	-	-	5.2	-	-	11	7	-	-	14	-	-	-	-	-
Yr9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-
Lr26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-
Sr31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-
Pm8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-
Sr21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13
Xmwg60	-	-	-	9.1	-	-	11	6	-	24	16	-	-	-	-	-
Sr33	-	-	13-18	-	-	-	-	-	-	30	-	-	-	-	-	13
Xmwg2245	-	-	-	-	-	-	-	-	17	-	-	-	-	-	-	-
Xmwg2083	-	-	-	11,7	-	-	-	-	-	32	19	-	-	-	-	-
Xbcd249	-	-	-	14.6	-	-	20	15-23	-	-	26	-	-	-	-	-
Xcdo388	-	15-19	-	14.6	24	-	-	-	-	32	-	39	-	-	-	-

Table 1. Continued.

Predicted order of markers	'Van Deynze 95 1A'	'Van Deynze 1B'	'Van Deynze 1D'	'Dubcovsky 95 1A/1A^m'	'Boyko 99 1D'	'Blanco 98 1A'	'Dub 95 1A^m G1777 × G2528'	'Dub 95 1A^m G3116 × DV092'	'Spielmeyer 00 1D SSP'	'Speilmeyer 00 1D LR'	'Dubcovsky 95 1B'	'Gill 93 1D'	'Lagudah 91 1D'	'Hart 93 1A'	'Hart 93 1B'	'Hart 93 1D'
Rf3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22	-
Gpi1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	18
Xmwg68	-	15-19	-	14.6	-	-	-	-	-	-	-	-	-	-	-	-
Xabc156	26	19-23	32	-	-	-	-	-	-	37	-	-	-	-	-	-
Gli3	29	19	-	14.6	-	-	21	15	-	-	-	-	-	42	29	-
Chs3	-	-	-	14.6	-	-	21	23	-	-	-	-	-	-	-	-
XksuF43	-	19-23	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xmwg584	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	-
XksuE18	32	25	-	19.7	60	-	-	-	-	-	-	47	38	-	-	-
XksuE19	-	-	-	-	65	-	32	-	-	-	-	41	-	-	-	-
Xbcd98/Xcdo99	37	-	-	27.5	73	-	-	34	-	-	-	-	-	-	-	-
5SDna1	-	-	-	27.5	-	-	-	34	-	-	47	-	41	-	-	-
XcslH69	-	-	-	30.1	-	-	32	-	-	-	47	-	43	-	-	-
Xpsr688	-	-	-	31.4	-	-	-	-	-	-	-	-	-	-	-	-
XksuG9	41	-	-	-	73-83	-	-	-	-	45	-	-	-	-	-	-
Xcmwg758	-	-	-	-	73-83	-	-	-	-	-	-	-	-	-	-	-
Xmwg67	44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xabg500	-	-	-	36.5	-	-	-	53	-	-	-	-	-	-	-	-
Xrz244	49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xcdo580	46	-	-	40.3	-	-	42	-	-	-	-	-	-	-	-	-
Yr15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	37	-
Tri	-	-	-	40.3	-	-	42	54	-	-	-	-	47	50	-	27
Xpsr381	-	-	-	-	-	-	-	-	-	-	47	-	-	-	-	-
Nor	-	36	-	-	-	-	-	-	-	-	47	-	-	-	40	-
Per1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	43	-
HK1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	43	38
Xcdo1173	-	-	-	41.6	-	-	44	-	-	-	-	-	-	-	-	-

'Van Deynze 95 1A' (Van Deynze *et al.*, 1995)
'Van Deynze 1B' (Van Deynze *et al.*, 1995)
'Van Deynze 1D' (Van Deynze *et al.*, 1995)
'Dubcovsky 95 1A/1A^m' (Dubcovsky *et al.*, 1995)
'Boyko 99 1D' (Boyko *et al.*, 1999)
'Blanco 98 1A' (Blanco *et al.*, 1998)
'Dub 95 1A^m G1777 × G2528' (Dubcovsy and Dvorak, 1995)
'Dub 95 1A^m G3116 × DV092' (Dubcovsy and Dvorak, 1995)
'Spielmeyer 00 1D SSP' (Spielmeyer *et al.*, 2000a)
'Speilmeyer 00 1D LR' (Spielmeyer *et al.*, 2000b)
'Dubcovsky 95 1B' (Dubcovsy and Dvorak, 1995)
'Gill 93 1D' (Gill *et al.*, 1993)
'Lagudah 91 1D' (Lagudah *et al.*, 1991)
'Hart 93 1A' (Devey and Hart, 1993)
'Hart 93 1B' (Devey and Hart, 1993)
'Hart 93 1D' (Devey and Hart, 1993)

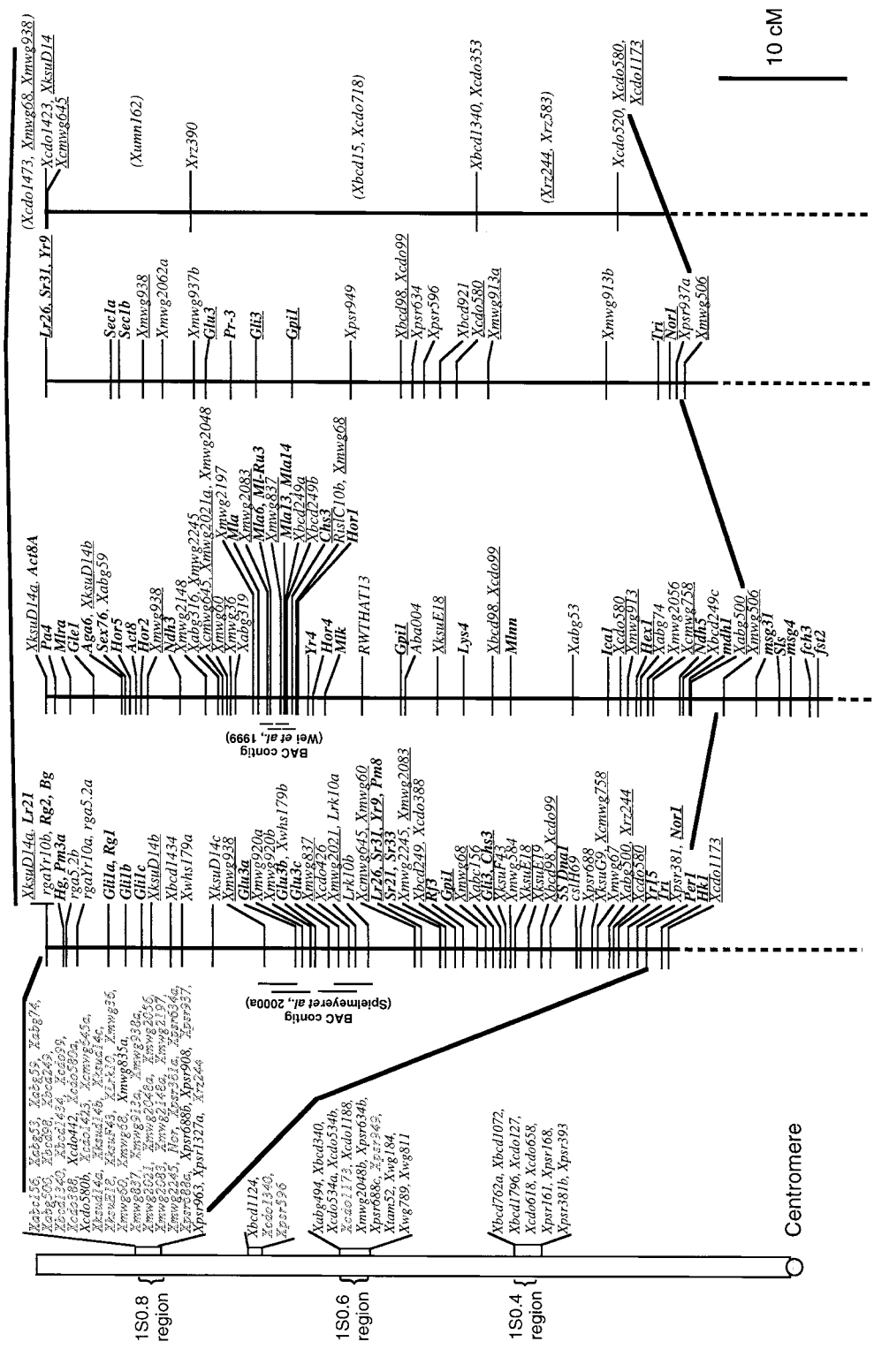

Figure 2. Consensus physical map for chromosome *1S* of wheat (Sandhu, 2000) in comparison with the genetic linkage map of oat (Van Deynze *et al.*, 1995) and consensus genetic linkage maps of wheat, barley, and rye. The marker loci shown in outline font on the consensus physical map are present on at least one of the genetic linkage maps. The marker loci common between two or more genetic linkage maps are underlined and genes are represented in bold letters.

Table 2. Genetic linkage maps of barley for '1S0.8 region'. Markers are arranged in their predicted order. (−) represents missing marker in that particular map.

Predicted order of markers	'Qi 96'	'Wei 99'	'Bezant 95'	'Graner 91'	'Kleinhof 93'	'Jensen 99'	'Langridge 95'	'Miyazaki 00'	'Graner 93'	'Kjaer 95'	'Franchowiak 97'
XksuD14a	-	-	-	-	-	-	-	0	-	-	-
Act8A	0.5	-	-	-	-	0	-	-	-	-	-
Pa4	-	-	-	-	-	0.7	-	-	-	-	0
Mlra	-	-	-	-	-	2.1	-	-	-	-	-
Gle1	-	-	-	-	-	4	-	-	-	-	3
Aga6	0	-	-	-	0	6.2	0	-	-	-	-
ksuD14b	-	-	-	-	-	-	1.4	18.5	-	-	-
Sex76	-	-	-	-	-	6.3	-	-	-	-	-
abg59	-	-	-	-	-	-	1.7	-	-	-	-
Hor5	2.1	-	-	-	1.4	7.7	3	-	0	-	-
Act8	-	-	-	-	2.1	8.5	2	-	-	-	-
mwg938	2.1	-	-	-	-	-	3.2	-	1.5	-	-
Hor2	3.2	0	0	0	2.8	8	3.7	-	0	0	7
Ndh3	-	-	-	-	-	11.4	-	-	-	-	-
mwg2148	5.2	-	-	-	-	13	6.6	-	2.9	-	-
abg316	-	-	-	-	-	14.4	-	-	4.4	-	-
mwg2245	-	-	-	-	-	-	-	-	4.4	-	-
mwg2021a	6.7	-	-	-	-	-	-	-	4.4	-	-
mwg2048	6.7	-	-	-	-	14.5	7.8	-	4.4	-	-
cmwg645	6.7	1	-	-	-	14.6	7.8	-	4.4	-	-
mwg60	-	2.1	-	-	-	-	-	-	-	-	-
mwg36	6.7	3.2	-	-	8.6	14.3	-	-	-	-	-
abg319	-	-	-	-	-	-	-	-	4.4	-	-
mwg2197	-	-	-	-	-	-	-	-	7.3	-	-
Mla	-	-	-	-	-	15.2	-	-	-	-	14
mwg2083	9.8	-	-	-	-	18	10.9	-	7.3	-	-
QEet.psb-1H	-	-	0-1.1	-	-	-	-	-	-	-	-
Mla6	-	4.4	-	-	-	18.1	11.1	-	7.3	14	-
Ml-Ru3	-	4.4	-	-	-	-	-	-	-	-	-
mwg837	11.6	-	-	-	13.3	18.6	12.1	-	8.8	-	-
Mla14	-	4.47	-	-	-	-	-	-	-	-	-
Mla13	-	4.47	-	-	-	-	-	-	-	-	-
bcd249a	-	6.07	-	-	-	-	-	-	-	-	-
bcd249b	-	6.37	-	-	-	-	-	-	-	-	-
Chs3	12.7	6.87	-	-	-	19.2	12.9	-	8.8	-	-
RislC10b	-	-	-	-	-	19.9	-	-	-	-	-
mwg68	-	6.67	-	-	-	-	-	-	-	-	-
Hor1	12.7	7.87	1.1	16.8	-	20.4	13.7	44.6	-	-	-
Yr4	-	-	-	-	-	21.3	-	-	-	-	-
Hor4	-	-	-	-	15.3	21.7	-	-	-	18	-
Mlk	-	-	-	-	-	22.7	-	-	-	-	22
RWTHAT13	19.2	-	-	-	-	26.1	19.2	-	16	-	-
Gpi1	-	-	-	-		28.8	-	-	-	35	-
Aba004	12.3	-	-	-	22.5	29.1	20.7	-	-	-	-
ksuE18	-	-	-	-	-	-	23.6	-	-	-	-
Lys4	-	-	-	-	-	-	-	-	-	-	31

Table 2. Continued.

Predicted order of markers	'Qi 96'	'Wei 99'	'Bezant 95'	'Graner 91'	'Kleinhof 93'	'Jensen 99'	'Langridge 95'	'Miyazaki 00'	'Graner 93'	'Kjaer 95'	'Franchowiak 97'
bcd98	28	-	-	-	-	-	28.1	-	-	-	-
cdo99	28	-	-	-	31.6	36.4	28.2	56.8	-	-	-
Mlnn	-	-	-	-	-	38.3	-	-	-	-	-
abg53	36.7	-	-	-	37.5	43	33.5	-	-	-	-
Ica1	37.7	-	-	-	43	47.3	37.9	-	-	-	-
mwg913	-	-	-	49.3	-	47	40.2	-	34.6	-	-
cdo580	-	-	-	-	-	-	43.7	-	-	-	-
Hex1	-	-	-	-	-	48.2	-	-	-	-	-
abg74	40.7	-	-	-	44.3	49	40.1	75.3	-	-	-
mwg2056	45	-	-	50.7	-	48.5	41.9	-	36	-	-
cmwg758	46.4	-	-	52.1	-	49.6	42.8	-	37.4	-	-
Ndh5	-	-	-	-	-	51.7	-	-	-	-	-
bcd249c	-	-	-	-	-	-	44	-	-	-	-
mdh1	-	-	-	-	-	52.5	-	-	-	-	-
abg500	-	-	-	-	49.6	52.6	-	81.8	30.3	-	-
mwg506	51.8	-	-	64.9		55.2	47.9	-	50.5	-	-
msg31	-	-	-	-	-	-	-	-	-	-	31-61
sls	-	-	-	-	-	-	-	-	-	-	31-61
msg4	-	-	-	-	-	-	-	-	-	-	31-61
fch3	-	-	-	-	-	-	-	-	-	-	31-61
fst2	-	-	-	-	-	62.7	-	-	-	-	61

'Qi 96' (Qi *et al.*, 1996)
'Wei 99' (Wei *et al.*, 1999)
'Bezant 95' (Bezant *et al.*, 1995)
'Graner 91' (Graner *et al.*, 1991)
'Kleinhof 93' (Kleinhof *et al.*, 1993)
'Jensen 99' (Jensen, 1999)
'Langridge 95' (Langridge *et al.*, 1995)
'Miyazaki 00' (Miyazaki *et al.*, 2000)
'Graner 93' (Graner *et al.*, 1993)
'Kjaer 95' (Kjaer *et al.*, 1995)
'Franchowiak 97' (Franchowiak, 1997)

of cytoplasmic male sterility (*Rf3*). Also contained in the region are some genes controlling morphology: glume color and morphology (*Bg, Rg1, Rg2, Hg*), glossy spike (*Gle1*), small lateral spikelet (*Sls*), chlorina seedling (*fch3*), fragile stem (*fst2*), and shrunken endosperm (*Sex76*), some other protein genes (*Gpi1, Chs3, Tri, Per1, Hk1, Act8, Act8A, Aga6, Ndh3, Ndh5, mdh1, Lys4, Ica1, Pr-3*), and a gene for preharvest sprouting (*Qphs.cnl*). The genes *Per1, Hk1, msg31, Sls, msg4, fch3*, and *fst2* are most probably also present in the '1S0.8 region', but their location was not confirmed. An additional 18 genes that were flanked by the '1S0.8 region'-specific markers, were not placed on the maps in Figure 2 because their precise location within the region was not known. In summary, we have identified 75 agronomically important genes for the '1S0.8 region' of various Triticeae species and have revealed their precise location within the region.

Table 3. Genetic linkage maps of rye for '1S0.8 region'. Markers are arranged in their predicted order. (-) represents missing marker in that particular map.

Predicted order of markers	'Korzun 98'	'Wang 92'	'Devos 96 '	'Wanous 97'	'Voylokov 98'	'Devos 93'	'Carrillo 92'	'Benito 90'	'Lawrence 86'	'Singh 90'	'Borner 98'	'Baum 91'
C Ter-1RS	-	-	-	-	-	-	-	-	-	-	-	0
cslH69.10	-	-	-	-	-	-	-	-	-	-	-	45
cslH69.13	-	-	-	-	-	-	-	-	-	-	-	65
Lr26	-	-	-	-	-	-	-	-	-	0	-	98
Sr31	-	-	-	-	-	-	-	-	-	0	-	98
Yr9	-	-	-	-	-	-	-	-	-	0	-	98
Sec-1a	-	0	-	-	-	0	0	0	-	5.4	-	103
Sec-1b	-	-	-	-	-	-	0.68	0.3	0	-	-	-
Xmwg938	0	-	-	-	0	-	-	-	-	-	0	-
Xmwg2062a	1.3	-	-	-	-	-	-	-	-	-	-	-
Xpsr937b	-	-	-	-	2.4	14	-	-	-	-	4	-
Glu3	-	-	0	-	-	-	-	-	-	-	-	-
Pr-3	-	-	-	-	-	-	-	10.5	-	-	-	-
Gli3	-	-	-	-	-	-	8.22	-	-	-	-	-
Gpi1	-	20	19.4	-	-	23	-	-	21.8	-	-	140
Xpsr949	-	-	-	-	-	0′	-	-	-	-	-	-
Xpsr634	-	-	-	0	-	6′	-	-	-	-	-	-
Xbcd98	-	-	28.9	-	11.2	-	-	-	-	-	12	-
Xcdo99	-	-	28.9	-	11.2	-	-	-	-	-	12	-
Xpsr596	-	-	-	10.6	-	7′	-	-	-	-	22	-
Xbcd921	-	-	-	11.9	-	-	-	-	-	-		-
Xcdo580	35.8	-	-	12.9	-	9′	-	-	-	-	30	-
Xmwg913a	36.2	-	-	-	30.6	-	-	-	-	-	30	-
Xmwg913b	46.5	-	-	-	-	-	-	-	-	-	-	-
Tri	-	-	9.3	-	-	-	-	-	-	-	-	150
Nor1	-	62	-	23	-	-	-	-	29.5	-	13.5	150
Xpsr937a	49.1	-	-	-	-	4'	-	-	-	-	33	-
Xmwg506	52.3	-	-	-	-	-	-	-	-	-	52	-

(′) represent recombination values after a break in genetic linkage map
'Korzun 98' (Korzun *et al.*, 1998)
'Wang 92' (Wang et al., 1992)
'Devos 96 ' (GrainGenes- http://wheat.pw.usda.gov/)
'Wanous 97' (Wanous *et al.*, 1997)
'Voylokov 98' (Voylokov *et al.*, 1998)
'Devos 93' (Devos *et al.*, 1993)
'Carrillo 92' (Carrillo *et al.*, 1992)
'Benito 90' (Benito *et al.*, 1990)
'Lawrence 86' (Lawrence and Appels, 1986)
'Singh 90' (Gaunt and Singh, 1990)
'Borner 98' (Borner and Korzun, 1998)
'Baum 91' (Baum and Appels, 1991)

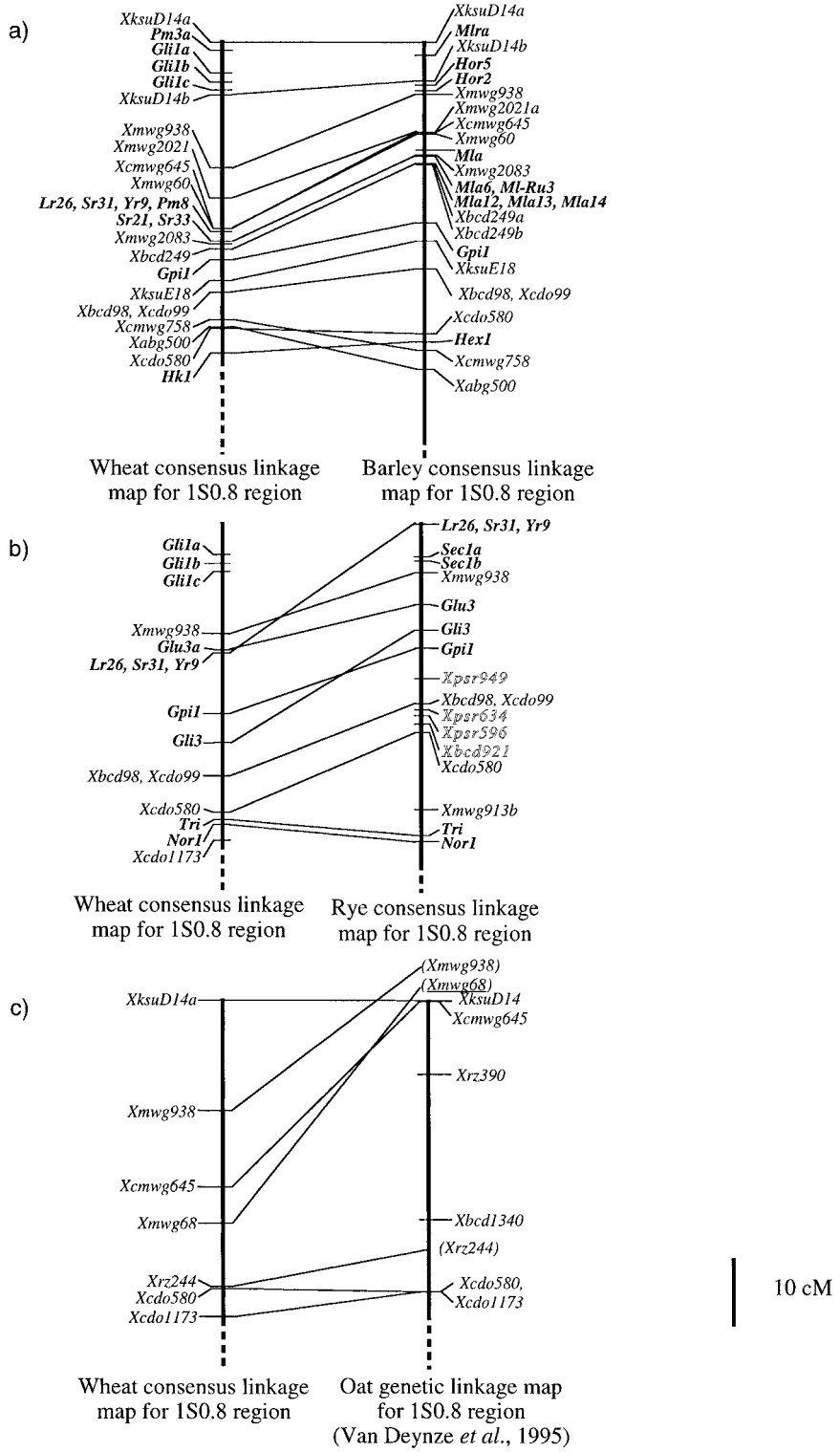

Figure 3. Comparison of the '1S0.8 region' among wheat, barley, rye and oat. a. Comparison of the wheat consensus linkage map for '1S0.8 region' with the barley consensus genetic linkage map. b. Comparison of the wheat consensus linkage map for '1S0.8 region' with the rye consensus genetic linkage map. c. Comparison of the wheat consensus linkage map for '1S0.8 region' with the oat genetic linkage map (Van Deynze *et al.*, 1995). The common markers are joined by lines. The genes are represented in bold letters. The markers shown in outline font do not map in the '1S0.8 region' on the wheat consensus physical map. Only the common markers between two maps are shown. Some of the genes that are not common to both maps are shown to represent the orthologous relationship between the two species.

Various map comparisons suggested orthologous relationships among many previously characterized useful genes of the Triticeae. Gliadins, secalins, and hordeins are the seed storage protein genes in wheat, rye, and barley, respectively. These are probably orthologous as the location of two of the gliadin gene loci (*Gli1a* and *Gli1b*) in wheat corresponds to that of two hordein loci (*Hor2* and *Hor5*) in barley and two secalin loci (*Sec1a* and *Sec1b*) in rye (Figures 3a and 3b). Similarly, the *Pm3a* gene of wheat and *Mlra* gene of barley have a similar map location (Figure 2) and may be orthologues. Both genes provide resistance to powdery mildew pathogens, *Pm3a* in wheat and *Mlra* in barley. Clustering of resistant genes has been observed in lettuce and other plants (Michelmore and Meyers, 1998). Many resistant genes are clustered in the '1S0.8 region' of wheat and barley too (Figure 3a). For example, four *Mla* genes of barley are present within 3 cM. In the corresponding region in wheat, however, only *Pm8* is present. In addition to *Pm8*, structural orthologues for other *Mla* genes are probably also present in wheat. The orthologues in wheat may be non-functional, providing resistance against different pathogens, or may have altogether different functions. Any of the three situations will make it difficult to establish an orthologous relationship between genes of closely related species such as wheat and barley. This and similar other examples exhibit the limitations of comparative genomics and accentuate the need for studying the gene of interest in the resident plant.

Structure of the '1S0.8 region' in Triticeae

Many differences in marker order were observed among wheat, barley, and rye. Except for *Xabg500* and *Xcmwg758*, the marker order was the same for wheat and barley (Figure 3a). Similar comparisons between wheat and rye revealed major chromosomal rearrangement(s). For example, three disease resistance genes (*Lr26, Sr31* and *Yr9*) that are present proximal to gliadin (*Gli1a, Gli1b* and *Gli1c*) and glutenin (*Glu3a, Glu3b* and *Glu3c*) gene loci in wheat are present in the most distal region in rye. The order of *Gpi1* and *Gli3* also was different in rye (Figure 3b). Few major discrepancies in marker order were also observed. For example, the marker *Xpsr596* is present between the '1S0.8 region' and the '1S0.6 region' on the physical map but is present in the middle of the '1S0.8 region' on the rye consensus genetic linkage map. Similarly, *Xpsr949* and *Xpsr634* are present in the '1S0.6 region' of wheat but among the '1S0.8 region' markers in rye. Marker locus *Xbcd921* physically maps on the long arm of group 1 chromosomes in wheat (data not shown), but is tightly linked to *Xcdo580* on the consensus rye map. Consensus wheat and oat map comparisons suggest that the region is poorly conserved even at low resolution. Some markers present in the '1S0.8 region' in wheat are also present in rye, but the order and distance between markers are not conserved (Figure 3c).

Many explanations may be proposed for these discrepancies in marker order and relative distances. Multiple loci or differences in probe sequence copy number among species may be one reason. Probe copy number differences were observed between wheat and barley (Namuth *et al.*, 1991). Many probes detected different numbers of loci in different plant genomes. For example, the probe KSUD14 detected three loci on wheat, two on barley and one on oat. The probe BCD249 detected two loci in barley, but only one in wheat. Comparisons between non-orthologous probe loci will falsely suggest rearrangements. In this study, however, differences in marker order were most likely not due to this. The consensus maps were constructed using mapping information from many maps, and it is highly unlikely to miss a locus.

The above observations suggest that at a gross level gene synteny is conserved among Poaceae genomes but many small chromosomal rearrangements exist which will only be revealed by detailed and precise analysis. Recent sequencing data showed that small rearrangements are very common even between closely related species. At low-resolution comparisons, the region containing the *Lr10* gene of wheat appeared to be conserved among barley, rice, and maize. Sequence data analysis revealed many small duplications, deletions, and inversions in all inter-specific comparisons (Feuillet and Keller, 1999). Similar results were observed during various other sequence comparisons among wheat, barley, rice, and maize (J. Bennetzen, personal communication).

Size of the '1S0.8 region'

The '1S0.8 region' is best localized on chromosome arm 1BS of wheat where it encompasses 10% of the satellite region. The satellite region is about 1 μ (68 Mb). Based on these calculations, the '1S0.8 region' should be ca. 7 Mb in size. The corresponding region in barley cannot be precisely localized because of the lack of translocation breakpoints, but it maps

between FL 0.67 and FL 0.88 of the translocation breakpoint-based physical map (Kunzel *et al.*, 2000). Genetically, the '1S0.8 region' in barley is about 20 cM (GrainGenes). The 1 cM region spanning the barley *Mla* cluster centered between markers *bcd249.1* and *mwg036* of the gene-rich region is about 1 Mb (Wei *et al.*, 1999). Physical-to-genetic distance, even within the *Mla* region, however, varies more than 10-fold, with 176 kb/cM being the most favorable ratio. Similar estimates for the two 110 and 270 kb subregions of the '1S0.8 region' in *Ae. tauschii* ranged from 20 to 270 kb/cM (Spielmeyer *et al.*, 2000a). Based on these estimates, the '1S0.8 region' could be anywhere from 1 Mb to 13.5 Mb. All things considered, an estimate of 7 Mb in wheat seems reasonable. The size of the region is probably the same among Triticeae species, as the distribution of markers and recombination is very similar.

Recombination within the '1S0.8 region'

The genetic length of the region was similar among wheat, barley, rye, and oat, and varied from 45 cM in oat to 50 cM in barley. In all four species, more than 80% of the short-arm recombination occurred in the '1S0.8 region'. For precise comparisons, maps containing only the common markers were developed for the four species (Figure 3). Relative recombination among markers was also very similar among the four species, although few localized differences were observed (Figure 2). For example, *Xbcd249* and *Gpi1* are 2 cM apart in wheat as compared to 9 cM in barley (Figure 3a). Localized differences in relative recombination were more pronounced between wheat and rye. Two markers, *Xcdo580* and *Tri*, are less than 2 cM apart in wheat but are 16 cM apart in rye (Figure 3b). This may actually be because of major rearrangement(s). In oat, markers *Xcmwg645* and *XksuD14* were perfectly linked, whereas they were 30 cM apart in wheat (Figure 3c).

It has been observed that recombination occurs mostly in the gene-rich regions (Gill *et al.*, 1996a, b; Schnable *et al.*, 1998; Sandhu *et al.*, 2001). Emerging sequence data suggest that recombination frequency varies manyfold even within a gene-rich region. Recombination in adjacent regions near seed storage protein loci in *Ae. tauschii* varied up to 13-fold (Spielmeyer *et al.*, 2000a). Likewise, the extent of recombination varied as much as 10-fold within a 1 Mb gene-rich region in barley (Wei *et al.*, 1999). Similar observations were made in the *Lrk10* region (C. Feuillet and B. Keller, personal communication). As stated earlier, the currently defined gene-rich regions are further partitioned into 'mini gene-rich regions' interspersed by gene-poor compartments. It would be interesting to study if the preferred sites of recombination coincide with the 'mini gene-rich regions'.

Structure of the wheat genome

Arabidopsis is a diploid with an estimated gene number of ca. 25 000. Although wheat is a hexaploid, the total number of genes is probably not three times that of *Arabidopsis*. Rough estimates based on the expression of morphological traits indicate that only about 19% of the wheat genes are expressed from all three genomes, 10% from two and 71% of the genes are expressed from only one of the three copies of the structural genes (Sandhu *et al.*, 2001). Homoeologues may have lost expression, acquired a different function, or may be providing environment or tissue specificity. So, the number of genes in wheat can be anywhere between 25 000 and 75 000. The gene-containing fraction of the wheat genome is about 1–3% because it is ca. 110 times larger than that of *Arabidopsis*. This estimate is probably accurate because similar values were obtained from the estimation of the gene-containing fraction based on the total number genes (25 000 to 75 000) with an average size of 2–4 kb. Using breakpoints of 300 deletion lines (example in Figure 1), the gene-containing regions of wheat were localized to about 10% of the chromosomal region. Therefore, only 10–30% of the currently demarcated gene-rich regions contain genes.

Each wheat chromosome is expected to contain an average of 1200–2400 genes, assuming a total of 25 000 to 50 000. The '1S0.8 region' probably contains 400–800 genes, 31% of the chromosome. These estimates suggest a gene density of a gene per 5 to 10 kb. The presence of orthologues among A, B, and D genomes will further increase the average gene density for the region. The total physical region spanned by genes averaging 2 kb in length will be 750–1500 kb, indicating that only 10–20% of the currently defined gene-rich region contains genes. Partial sequence analyses of the '1S0.8 region' support these estimates as the gene density varied from a gene every 4.6 kb to 20 kb (Rahman *et al.*, 1997; Panstruga *et al.*, 1998; Feuillet and Keller, 1999). These estimates suggest that the '1S0.8 region' is further partitioned into 'mini gene-rich regions' interspersed by gene-poor regions.

Conclusions

Low-density comparative mapping suggested that genome organization and gene order is collinear among the members of the Triticeae (Ahn *et al.*, 1993; Moore *et al.*, 1995; Bennetzen and Freeling, 1997). This study and the emerging sequence data show that small deletions, duplications, and inversions, along with occasional major rearrangements, are very common even among closely related species. These small rearrangements are below the detection level of low-density comparisons, and thus were not revealed earlier. These observations may explain unsuccessful attempts to clone the *Ph1* gene of wheat and the *Rpg1* gene of barley using rice as a model (Foote *et al.*, 1997; Kilian *et al.*, 1997). As demonstrated in many previous studies (Van Deynze *et al*, 1995; Faris *et al*., 2000; Sandhu *et al*., 2001), comparative mapping is very effective for targeted marker enrichment. Detailed genomic exploration should, however, be performed in the resident plants. It was very interesting to note that the small rearrangements usually did not affect recombination frequencies. Occasional and localized major differences in recombination frequency are worth studying further.

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